Limnol. Oceanogr., 38(3), 1993, 547–560

An algal carbon budget for pelagic-benthic coupling in Lake Michigan

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Abstract

A budget for algal carbon was constructed to quantify the magnitude and major pathways of pelagic-benthic coupling at a site in southeastern Lake Michigan. The flux of algal C to the benthos and the rate of carbon burial were estimated from sediment traps and dated sediment cores, respectively. Assimilation and respiration rates of *Diporeia* sp., an abundant benthic amphipod, and of sediment microheterotrophs were measured in a microcosm study with ^{14}C-labeled algae (*Melosira italica*). *Melosira* (*italica* and *islandica*) accounted for 53% of the algal C flux to the sediments. Radionuclide concentrations indicated no net sediment burial of organic C. Of the total C assimilated by *Diporeia,* 60% was respired, 35% was incorporated into biomass, and 5% was accounted for as soluble dissolved organic compounds. The areal rate of *Diporeia* respiration (29 nmol C cm $^{-2}$ d^{-1}) was 23 times greater than that for sediment bacteria (1.3 nmol C cm^{-2} d^{-1}). Release of radioisotope in the form of dissolved organic compounds was much lower than that incorporated and respired for both *Diporeia* and sediment bacteria. Of the 61 mmol C m^{-2} of algal C estimated to be deposited during the spring bloom, *Diporeia* assimilation accounted for 61%, significantly more than the 2% observed for microbially mediated algal decomposition. These observations support the hypothesis of a strong pelagic-benthic energy coupling between the spring diatom bloom and *Diporeia* in Lake Michigan.

The magnitude of pelagic-benthic coupling in aquatic environments is constrained by how efficiently energy, in the form of biochemical compounds such as lipids, carbohydrates, and proteins, is transferred spatially from the pelagic to the benthic zone and between trophic levels. In Lake Michigan, average particle residence times in the water have been estimated with radionuclides to be on the order of a few weeks (Eadie et al. 1984). However, large algal inputs during the spring bloom may be important in rapidly supplying high-energy, easily metabolizable material to even the deepest depositional basins in a matter of hours or days. The fate of this material is determined largely by uptake rates and assimilation efficiencies of benthic macroinvertebrates, meiofauna, and microbial heterotrophs. The extent to which bacteria remineralize fresh organic detritus, thereby acting as an energy sink, necessarily constrains the amount of energy that can be directly transferred to benthic invertebrates and hence to higher trophic levels. Also, if sufficiently abundant and metabolically active, benthic invertebrates may play a significant role in organic matter mineralization through respiration and excretion (Gardner et al. 1987). Therefore, to understand the fate and effects of particles settling from the spring diatom bloom, it is important to determine both the amount of metabolizable organic matter reaching the sediment–water interface and the pathways of organic matter assimilation and mineralization.

Diporeia sp. (formerly called *Pontoporeia hoyi*; *see* Bousfield 1989) is an important component of benthic-pelagic coupling in Lake Michigan for several reasons. This amphipod accounts for 65% of total benthic biomass at depths >30 m in southern Lake Michigan (Nalepa 1989). It is a favored prey item for most Great Lakes forage fish including rainbow smelt

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Acknowledgments

We thank Gary Fahnenstiel for advice on algal labeling and enumeration and for providing the labeled bicarbonate, Gerald Bell for assistance in construction of the sediment traps, Peter Landrum and his students for assistance with animal collection, John Robbins for use of the well detector and comments on the manuscript, Brian Eadie, Glenn Lopez, and James Cotner for comments on the manuscript, Rick Carlton for unpublished dissolved oxygen data and comments, John Lehman for ship time, and the captains and crew of the RV *Shenehon* and the RV *Laurentian* for field assistance.

This work was supported by the National Research Council through a postdoctoral fellowship to S.A.F. The U.S. Geological Survey provided logistical support during the final preparation of the manuscript.

GLERL contribution 783.

(*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and bloater (*Coregonus hoyi*) (Wells 1980). On the basis of summer inputs extrapolated to annual rates, *Diporeia* have been estimated to assimilate up to 30% of incoming organic material (Gardner et al. 1985). *Diporeia* has relatively high lipid levels, which increase to almost half of the animal's ash-free dry weight immediately after the spring diatom bloom (Gardner et al. 1985). Thus, *Diporeia* is likely an important link in the rapid transfer of organic C and possibly lipophilic contaminants up the food chain. For example, *Diporeia* collected from southeastern Lake Michigan accumulated selected polycyclic aromatic hydrocarbons and polychlorinated biphenyl congeners (Landrum 1988 and references within).

On the basis of studies that identified *Diporeia*'s preference for fine-grained sediments rich in bacteria, *Diporeia* was thought to obtain the bulk of its carbon and energy from detritus and sediment-associated microbes (Marzolf 1965). Further support for this notion came from gut content analyses of *Diporeia* (and closely related genera) that seemed to indicate that detritus and bacteria accounted for 98–99% of all C sources (Johnson 1987; Evans et al. 1990). Recent work, however, has shown that *Diporeia* readily ingests whole diatom cells, and that extensive trituration and digestion of this material makes gut analysis of very limited value (Quigley and Vanderploeg in press). Moreover, for various common macrofauna, theoretical calculations indicate that bacteria alone are insufficient sources of energy (Baker and Bradnam 1976; Cammen 1980; Findlay and Meyer 1984). Also, certain essential amino acids (e.g. methionine and perhaps arginine, histidine, and lysine) and essential polyunsaturated fatty acids needed for macrofaunal growth are not present in bacteria (Phillips 1984).

Diatoms, on the other hand, are especially good sources of these compounds. Benthic macrofaunal growth in general, and *Diporeia* growth in particular, has been linked with sedimentation of the spring diatom bloom in freshwater (Johnson 1987, 1988) and marine (Graf et al. 1982; Rudnick 1989) systems. Diatoms can supply the bulk of annual energy requirements for benthic macrofaunal production (Christensen and Kanneworff 1986; Grassle et al. 1985). Spring algal assemblages in Lake Michigan are dominated by large diatoms such as *Melosira italica* and *Melosira islandica* (Fahnenstiel and Scavia 1987). Importantly, sinking of these large cells accounts for >95% of algal losses annually from the epilimnion at an offshore site in Lake Michigan. In Lake Michigan, the spring diatom bloom may supply as much as a third of the energy required annually for *Diporeia* production (Gardner et al. 1990). Finally, the relatively high lipid content (~40% of cell carbon) of *M. italica* (Fitzgerald unpubl. data) can be readily exploited as an energy source by *Diporeia*.

The objective of the present study was to construct an algal C budget for a nearshore area in the lake to balance the input of fresh carbon (mainly sinking diatoms) with losses including assimilation by benthic amphipods (incorporation, respiration, and release of dissolved organic compounds), respiration by sediment microheterotrophs, and burial in the sediments (Table 1). This site was chosen because near-maximal *Diporeia* abundances of ~11,400 animals m^{-2} occur in this region (Nalepa et al. 1988; Quigley and Lang unpubl. data). This study quantifies benthic-pelagic coupling with a combination of field measurements (trap sampling to estimate diatom flux to the sediment and core analysis to estimate C burial) and an experimental approach (microcosm study) to measure assimilation and respiration rates of both *Diporeia* and sediment microheterotrophs at one site in southeastern Lake Michigan.

Methods

Study site—All trap material, sediments, amphipods, and bottom water were collected in 1990 from a 45-m-deep station located off Grand Haven (43°1′6″N, 86°19′35″W) during cruises aboard the RV *Shenehon* or the RV *Laurentian* (Fig. 1). This site is located in the slope region of Lake Michigan as defined by Eadie et al. (1984) and is on the edge of a local depositional basin directly to the west (J. Robbins pers. comm.).

Sampling and analysis—Inputs of algal C to the benthic environment were quantified with sediment traps during the 1990 spring bloom. Trap arrays were deployed twice covering the period from 12 April through 29 June. A 20.3-

Table 1. Parameters making up the algal carbon budget and how they were measured.

Budget parameter	How measured
Spring diatom bloom	Sediment traps
Diporeia assimilation (microcosm study)	
Incorporation	^{14}C biomass
Respiration	$^{14}CO_2$ production
Excretion	[^{14}C]DOC
Sediment bacteria (microcosm study)	
Algal decomposition	[^{14}C]POC loss
Respiration	$^{14}CO_2$ production
Net release of dissolved metabolites	[^{14}C]DOC
Burial	Dated cores

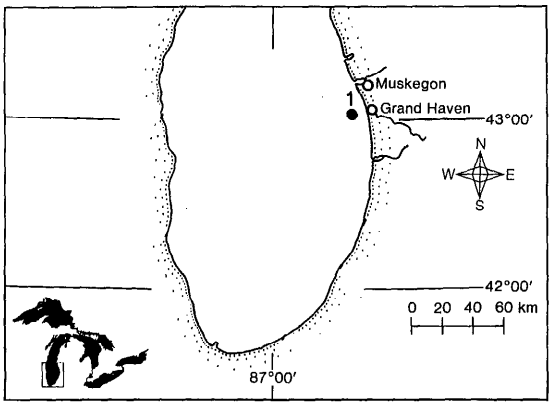

Fig. 1. Map showing location of study site.

cm-diameter trap (5 : 1 aspect ratio), deployed 5 m above the bottom, was identical in design to those used by Eadie et al. (1984). Each trap consisted of an opaque PVC tube with a funnel above a 500-ml plastic sample bottle that was screwed into the threaded lower portion of the trap. Algal material for taxonomic analysis and enumeration of algal cells was preserved with Lugol's solution (2% final concn) that was added to the collection bottles before the traps were deployed.

Sample bottles were removed from the traps and kept on ice (~4 h) during transit back to the laboratory, where they were amended with 1% (final concn) formaldehyde to preserve algal cells and stored at 4°C in the dark. Bottles were shaken to uniformly mix the contents, and the total volume in each was determined with a graduated cylinder. A subsample was immediately removed, diluted, and filtered for taxonomic analysis and cell enumeration (done by L. Feldt). All algae on the filter were keyed out to the species level and counted. Cell counts were converted to cell fluxes by dividing cell numbers by the product of deployment days and the collection area of the trap. The flux of algal C was calculated as the product of cell flux and known C contents from previously determined cell volumes (Strathmann 1966). Calculated algal C fluxes measured in the trap 5 m off the bottom were assumed to approximate those at the sediment–water interface.

Surficial sediments were sampled for solid-phase constituents with a 7.62-cm-diameter gravity corer. The core was immediately sectioned on-board ship at 1-cm intervals down to 10 cm, and at 2-cm intervals thereafter downcore. Sections were placed in 125-ml wide-mouthed plastic bottles and kept on ice for ~4 h, until they could be dried (60°C) to a constant weight and then pulverized.

Depth distributions of total organic C (TOC) and total N (TN) were determined on portions of dried sediments with a Perkin Elmer CHN elemental analyzer. Inorganic C was removed before analysis by adding 50 μl of 3 N H_3PO_4 directly to the sample boats. TN was determined on unacidified samples. All samples were analyzed in duplicate with relative errors usually <5%.

Biogenic silica was determined with a modification of the timed extraction procedure of DeMaster (1981), and replicate samples had a 3% relative SE. Weight percent sand was determined by wet-sieving a 1-g portion of the dried sediment through a 63-μm sieve and subsequently weighing the retained portion. Replicate samples had a relative SE of 3.9%.

The bulk sediment accumulation rate was estimated from depth distributions of ^{210}Pb ($t_{1/2}$ = 23 yr) and ^{137}Cs ($t_{1/2}$ = 30.2 yr) activities (in dpm g^{-1}) (Robbins and Edgington 1975). Accumulation of very recently deposited sediments was monitored by the presence of ^{7}Be ($t_{1/2}$ = 54 d). All three isotopes were determined directly on a 4-g portion of dried, pulverized sediments in plastic counting vials with a high-purity germanium detector coupled to a multichannel analyzer (Larsen and Cutshall 1981). The detector efficiency for each radioisotope was calculated from activities determined on a calibrated lithium-drifted germanium detector also coupled to a multichannel analyzer.

Porosity (ϕ, in ml_{pw} ml_{ws}, where pw is pore water and ws is wet sediment) was calculated from the water content (weight loss upon drying) and an assumed dry sediment density of 2.45 g cm_{ds}^{-3} (where ds is dry sediment).

A unialgal culture of *M. italica* (provided by Norman Andresen) was inoculated into four 1-liter sterile tissue culture flasks containing WC medium (Guillard and Lorenzen 1972). One milliCurie of $NaH^{14}CO_3$ (NEN; sp act = 40–60 mCi ml^{-1}) was added to each of three flasks, and the diatoms were cultured at 15°C under a 14 : 10 L/D cycle with daily agitation. Radiocarbon incorporation into the algal biomass was monitored daily by liquid scintillation counting of 1 ml of acidified culture medium added to 10 ml of scintillation cocktail on a Packard Tri-Carb liquid scintillation counter. Activities (in dpm) were corrected for quenching with external standards. When no further incorporation of radioactivity was detected (after 8 d), the cells were harvested and rinsed with autoclaved, distilled, demineralized water until the radioactivity of the supernate no longer decreased. The cells were resuspended in a minimum volume of water and stored frozen until needed. Even after being thawed and refrozen five times, ~95% of the label in the algal suspension was associated with particles, as determined via filtration (0.22-μm pore-size Anopore). The specific activity of this algal suspension, determined by triplicate direct injections into scintillation cocktail, was 1.1 μCi (μmol algal C)$^{-1}$.

Diporeia was collected with a ponar grab sampler in conjunction with elutriation onboard ship (Nalepa 1987). The animals were transported back to the lab on ice (~4 h) and immediately transferred to shallow plastic aquaria containing surficial sediment and bottom water from the station. The animals were kept in the dark at 4°C for 102 d. Animals used in the microcosm study were gently sieved out of the sediment, and three individuals were randomly added to each of several microcosms 24 h before radiolabeled algae were added (*see below*).

About 2 liters of surficial sediments were collected with a Soutar-type box corer. The top 0–1 cm of the core was gently siphoned into a clean polyethylene Erlenmeyer flask trap. The sediments were kept on ice during transport back to the lab and then wet-sieved (63-μm mesh) to remove macrofauna with a small amount of bottom water collected from the site to rinse the sediment through the sieve. The sieved sediments were allowed to settle overnight and then adjusted to the in situ porosity (determined from the core sample, *see above*). The overlying water was carefully removed and the sediments were stored at 4°C in the dark for 18 d. Several liters of bottom water were collected with a bottom-tripping Niskin bottle, returned to the lab, and kept at 4°C in the dark.

The microcosm study consisted of examining the fate of algal C over a 60-d time-course in the presence of either three unsexed, actively swimming *Diporeia* (+A treatment) or 10 ml of surficial sediments and their associated microheterotrophs (+S treatment). The experimental animal density was ~25% of that in the field. Microcosms consisted of clean 60-ml septum vials with bottom surface areas of ~10 cm^2. Thus the sediment layer in the microcosms was 1 cm deep. The animals were carefully placed into 40 ml of bottom water in the +A treatment and allowed to acclimate overnight in the vials for 24 h before adding labeled algae. The sediments were carefully pipetted into the bottom of the vials of the +S treatment, and 40 ml of bottom water were added slowly to avoid sediment resuspension. Several (72) replicate microcosms were assembled, inoculated with 140 μl (1.5 μCi containing 1.38 μmol C in 371,000 cells) of the labeled algal suspension, closed, and incubated at 4°C in the dark. This addition was equivalent to ~9 d of sedimentation of *M. italica* and *M. islandica* on a 10-cm^2 area as measured in a trap suspended about 5 m off the bottom in April–June 1990. Proportionately fewer algae than would be deposited during the entire bloom were added to each microcosm in keeping with the lower areal density of experimental animals as compared to that in the field. Thus, the microcosm study and the field had similar algae : animal ratios when considered over the entire time-course. Triplicate vials of each treatment were killed at 0, 1, 3, 8, 14, 21, 41, and 60 d. The six zero-time samples (triplicates for each treatment) were processed within 2 h of adding label. No *Diporeia* mortality occurred during the microcosm study.

In a third treatment, microcosms contained both sediments and animals (+A+S). The animals in this treatment did not ingest the added

algae, but instead immediately burrowed into the sediments and remained there for the duration of the time-course. Rates of $^{14}CO_2$ production and [^{14}C]POC decomposition were similar to those observed in the +S treatment. Because the kinetics of CO_2 production and algal decomposition were similar in the +A+S and +S treatments, we concluded that ambient oxygen was likely depleted in these treatments to a level where *Diporeia* metabolism was affected. To test this assumption, we estimated the flux of oxygen into the sediments with Fick's first law and concentration gradients obtained from oxygen profiles measured with an oxygen microelectrode at this station (R. Carlton unpubl. data). The oxygen diffusivity in pore water was assumed to be 1.4×10^{-5} cm^2 s^{-1}, and the measured sediment porosity was 0.65. This calculation indicated that the minimum and maximum oxygen gradients were ~0.56 and ~1.05 μM O_2 cm^{-4}, respectively, corresponding to oxygen uptake rates of about −4.4 and −8.3 μM d^{-1} for the 10-cm^2 sediment surface area of the microcosms.

All oxygen in the overlying water would have been depleted after the first 2 d, assuming conservatively that the water in the microcosms was saturated with oxygen at the beginning of the experiment. This analysis arbitrarily assumed that oxygen gradients and consumption rates in the homogenized sediments of the microcosms were the same as those measured on intact cores. However, these calculated oxygen fluxes were conservative because the concentration gradient was not measured with enough resolution to evaluate the microgradient at the sediment–water interface. The concentration gradients underestimate the true oxygen flux at the sediment–water interface where the diffusivity is greater than in deeper sediments (R. Carlton pers. comm.). Considering that the estimates of the concentration gradient were conservative, we concluded that oxygen was rapidly removed from the water in the +A+S microcosms during the initial few days. Because oxygen depletion inhibits *Diporeia* metabolism (Quigley et al. in prep.), we did not further consider results from these microcosms.

At each time point, respective vials were opened, and the overlying water was quickly and carefully decanted into bottles. These bottles and the original septum vials containing sediments were closed, 1 ml of an acidified solution of formaldehyde (62.5 ml of H_2SO_4 and 67.5 ml of 40% formaldehyde in 1,000 ml) was injected through septa, and the containers were vigorously agitated several times over 24 h. Volatilized $^{14}CO_2$ from the overlying water and sediment pore water was collected onto a filter paper suspended from the cap and soaked with 0.2 ml of phenethylamine. After 24 h, the bottles and vials were opened, the filter papers were transferred to scintillation vials containing 10 ml of cocktail, and activity was determined on a scintillation counter as described previously. All activities were corrected for bicarbonate recovery efficiency from both overlying water and sediment pore water.

After $^{14}CO_2$ was stripped out of solution, overlying water from +S treatment vials was centrifuged (10 min at 10,000 × *g*) to recover sediment particles and residual labeled algae, and the supernate was filtered (0.2-μm Anopore) into clean glass vials. Animals from the +A treatment vials were removed before centrifugation, rinsed for 1 min with distilled water, dried (60°C for 2 d under nitrogen) in preweighed glass microculture tubes, and stored until further analysis. Sediments were rinsed into their associated centrifuge tubes containing recovered particles. Pore water was recovered after centrifugation and filtered into clean glass vials. The sediments were then dried (60°C), pulverized, and stored for later analysis (*see below*). Activity of [^{14}C]DOC was determined on portions of the overlying water (for +A and +S treatments) and on the pore water (for +S treatment).

Radioactivity incorporated into *Diporeia* biomass was assayed by homogenizing two randomly chosen animals from each microcosm in 0.3 ml of 2 : 1 methanol : chloroform. The homogenate was diluted, and a portion was assayed for radioactivity. [^{14}C]POC in both treatments was determined by difference after summing all other fractions because direct determination of [^{14}C]POC in sediments was consistently underestimated (Fitzgerald unpubl. data).

Relative standard errors, expressed as percentages of the means, for all radiolabeled fractions were calculated for triplicate vials and, as such, represent the maximum error associated with the entire protocol for those de-

Table 2. Average relative standard errors for all radiolabeled fractions collected in the microcosm study.

Radiolabeled fraction	Avg relative SE
Overlying water	
$^{14}CO_2$	7.4
[^{14}C]DOC	8.7
Pore water	
$^{14}CO_2$	8.2
[^{14}C]DOC	3.5
^{14}C *Diporeia*	48.5
Sediment [^{14}C]POC	9.8

terminations (Table 2). Errors were <10% for all radiolabeled fractions except ^{14}C *Diporeia,* which had a relative error of almost 50% reflecting the high variability of individual animals from the triplicate microcosms.

Results

Fluxes of algal cells and carbon—Fluxes of algal cells (in cells cm^{-2} d^{-1}) for the most abundant algal species identified in the trap material from the two deployments are shown in Fig. 2. Thirteen diatom species accounted for >99% of all cells counted. *M. italica* and *M. islandica* were most abundant during both deployment periods, with fluxes ranging from ~5,200 to 8,800 cells cm^{-2} d^{-1}. Together, these two species accounted for ~54% of all cells for the entire sampling period. Other large diatoms, including *Tabellaria fenestrata, Fragilaria crotonensis, Fragilaria intermedia* v. *fallux, Asterionella formosa,* and *Stephanodiscus* sp., accounted for most of the remaining cells.

Melosira (*italica* and *islandica*) also dominated the flux of algal C measured during both trap deployments (Fig. 2). Carbon fluxes for these two species ranged from ~37 to 45 nmol cm^{-2} d^{-1} for the entire deployment period, representing ~53% of the total algal C flux. Much of the remaining flux was accounted for by *T. fenestrata, F. crotonensis, F. intermedia* v. *fallux,* and *A. formosa.* Although the total algal C flux accounted for <1% of the TOC flux at this site during the sampling period (unpubl. data), this labile C may drive a relatively large proportion of benthic metabolism.

Sand, TOC, TN, and biogenic silica sediment depth distributions—Depth distributions of sand, TOC, TN, and biogenic silica (in wt%)

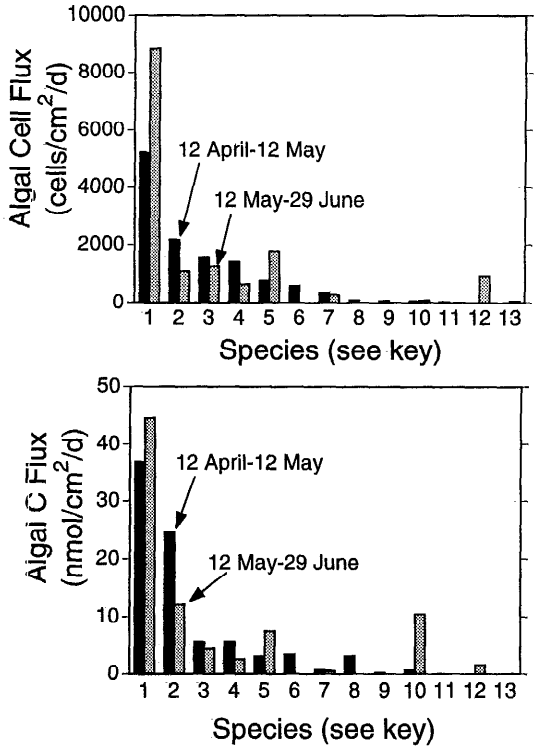

Fig. 2. Fluxes of algal cells and C calculated for the 13 most abundant algal species identified in trap material. 1. *Melosira* (*italica* + *islandica*); 2. *Tabellaria fenestrata*; 3. *Fragilaria crotonensis*; 4. *Fragilaria intermedia* v. *fallux*; 5. *Asterionella formosa*; 6. *Stephanodiscus transilianicus*; 7. *Fragilaria capucina*; 8. *Synedra ulna*; 9. *Synedra ostenfeldii*; 10. *Cyclotella compta*; 11. *Cyclotella comensis*; 12. *Stephanodiscus* sp.; 13. *Stephanodiscus minutus.*

plotted against cumulative mass (in g cm^{-2}) in the sediments are shown in Fig. 3. The sediments are silty sands, with ~60–70% of the dry weight accounted for by sand-sized particles (>63 μm). Biogenic silica decreased rapidly and linearly from ~1 wt% at the sediment–water interface to ~0.15 wt% at 3.5 cm. Below this depth, biogenic silica remained fairly constant, averaging ~0.3 wt%. This profile probably reflects recent deposition and rapid mixing of diatom frustules into surficial sediments.

Concentrations of both TOC and TN were low and fairly uniform with depth. TOC concentrations decreased from ~0.6 wt% at the surface to ~0.4 wt% within the upper few centimeters. TN was extremely low, averaging ~0.1 wt% in the upper several centimeters (near the detection limit for our measure-

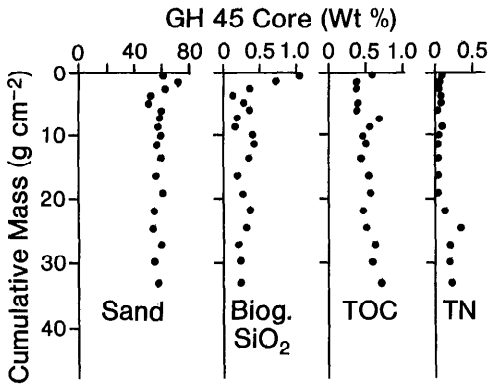

Fig. 3. Depth distributions of sand, biogenic silica, TOC, and TN at the study site.

ments). On the basis of ^{210}Pb and ^{137}Cs depth distributions (data not shown), the net sediment accumulation rate was negligible (i.e. $\lesssim$0.03 cm yr^{-1}). However, the presence of measurable ^{7}Be (a cosmogenic radionuclide) in the upper 2 cm (unpubl. data), in addition to virtually all of the excess ^{210} Pb and ^{137}Cs, suggests that recent, short-term deposition of freshly labeled material reaches the sediment surface and is mixed down into the upper sediments. Thus, organic matter reaching the sediment surface is ingested, mineralized, or resuspended and deposited elsewhere, with virtually none being buried.

Microcosm study—Decomposition of the labeled algae ([^{14}C]POC, as a percentage of the total added label) in the +S and +A treatments over the 60-d time-course is shown in Fig. 4. [^{14}C]POC was decomposed rapidly in the +A treatment, decreasing exponentially

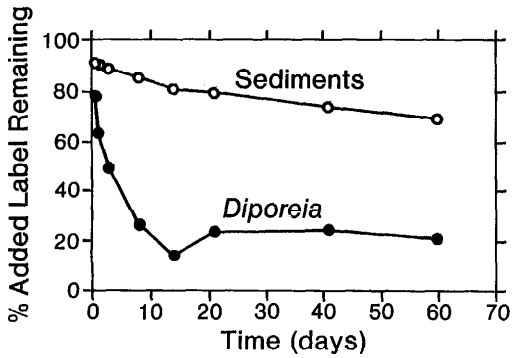

Fig. 4. Decomposition of the labeled algae ([^{14}C]POC) by *Diporeia* or sediment microbes during the 60-d time-course.

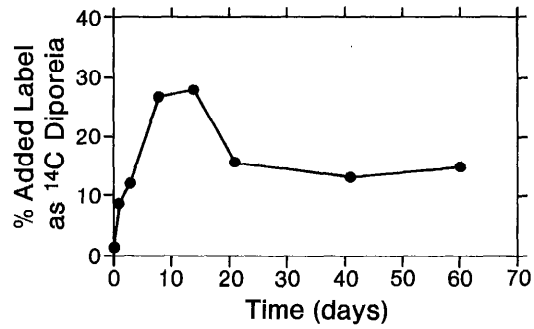

Fig. 5. Incorporation of labeled algal C in *Diporeia* biomass.

from ~80% at the beginning of the time-course to ~15–25% after 2 weeks. In contrast, [^{14}C]POC decreased much more slowly in the +S treatment, resulting in a loss of only ~10% within the first 2 weeks. After this time and until the end of the time-course, [^{14}C]POC was continually decomposed albeit at a slightly slower rate. Surprisingly, after 60 d, ~70% of the added label remained as [^{14}C]POC in the +S treatment.

Incorporation of labeled algal C in *Diporeia* biomass (as a percentage of the total added label) is shown in Fig. 5. The three animals in each vial incorporated a maximum of ~27% of the added label after 2 weeks. After this time, the label recovered in the animals decreased to ~15% during the third week, and thereafter remained fairly constant. The lack of label incorporation after 2 weeks corresponds to the time when oxygen should have become limiting to *Diporeia* metabolism. This time was calculated a priori to be ~8 d, assuming oxygen saturation at the beginning of the time-course and using experimentally determined respiration rates measured for *Diporeia* at the same temperature (4°C) (Quigley et al. in prep.). Also, ~12% decrease in labeled *Diporeia* biomass after the first 2 weeks could be explained by a lack of feeding and loss of previously incorporated labeled C.

$^{14}CO_2$ production (as a percentage of the total added label) was much more rapid in the +A treatment than that in the +S treatment during the initial 3 weeks of the time-course (Fig. 6). Production rates of $^{14}CO_2$ in the +A treatment declined from a relatively rapid rate during the initial 3 d, to a slightly slower one between 3 d and 3 weeks, and finally to a much slower rate that remained fairly constant until

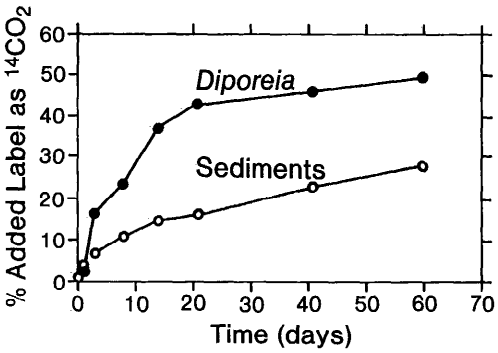

Fig. 6. Total $^{14}CO_2$ production during the 60-day time-course. ($^{14}CO_2$ in pore water and overlying water has been summed for the +S treatment.)

the end of the time-course. After 60 d, the animals (and associated microbes) had respired about half of the total added label. In contrast, $^{14}CO_2$ production rates in the +S treatment were much slower than in the +A vials at all time points and decreased exponentially over the time-course. After 60 days, $^{14}CO_2$ accounted for ~28% of the added label, equivalent to about half the amount observed in the +A treatment.

[^{14}C]DOC concentrations (as a percentage of the total added label) were ~2–4-fold higher in the +A as compared to the +S treatment (Fig. 7). In the vials containing *Diporeia,* [^{14}C]DOC accounted for ~20% of the added label, increasing slightly over the initial week and then decreasing throughout the remainder of the study. [^{14}C]DOC in these vials represents not only possible excretion of labeled [^{14}C]DOC by the animals, but also any "sloppy" feeding losses or autolytic decomposition of the labeled algae. Because it is a nearly uniform percentage of the total added label (including at time 0), this result may represent rapid autolytic decomposition of the labeled algae (within the first 2 h that were required to process the first samples) rather than excretion by the animals. The slight increase in [^{14}C]DOC during the first week could possibly be due to animal excretion, however it only accounted for a maximum of ~5% of the added label. [^{14}C]DOC concentrations in the +S treatment decreased throughout the time-course from ~8% at the beginning to ~4% after 60 d, likely due to microbial degradation.

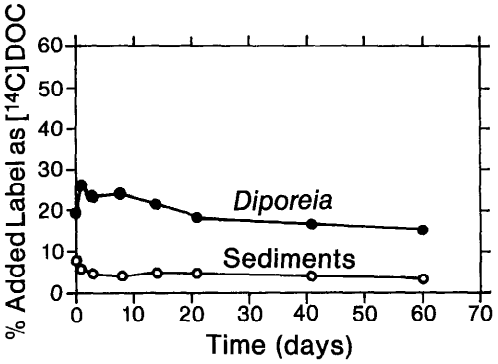

Fig. 7. Net [^{14}C]DOC production-release during the 60-d time-course. ([^{14}C]DOC in pore water and overlying water has been summed for the +S treatment.)

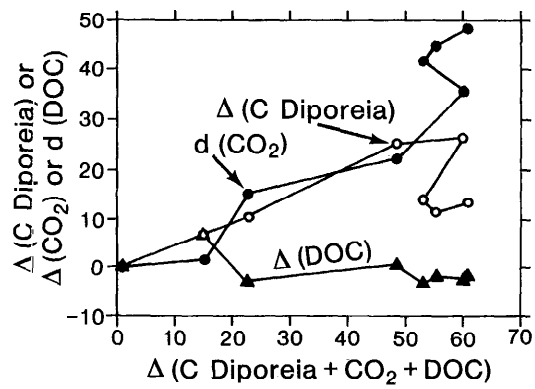

Fig. 8. Changes in ^{14}C incorporation, respiration, and excretion as a function of the change in assimilation [Σ(incorporation + respiration + excretion)].

Discussion

Diporeia *assimilation rate measurements—methodological considerations*—The accuracy of our carbon assimilation rate measurements on *Diporeia* relies on three main assumptions, namely that bacterial metabolism was relatively low in the +A treatment, that bottle effects (e.g. oxygen depletion) were not important, and that feeding rates in the laboratory would be comparable to those in the field. Although the +A vials were not axenic, there are several reasons to believe that observed $^{14}CO_2$ production and label incorporation during the first week or so in these vials were largely due to *Diporeia* metabolism rather than to bacterial respiration. First, incorporation, respiration, and organic compound release rates were fairly constant during this period (Fig. 8) when calculated ambient dissolved oxygen

levels could sustain normal metabolic rates (*see above*). *Diporeia* incorporation and respiration rates decreased sharply after this time presumably due to reduction of the oxygen concentration below a minimum level (Quigley et al. in prep.). Had bacterial metabolism been important, observed and calculated decreases in the rate of label incorporation would probably not have been as coincident. Second, although orders of magnitude more bacteria should have been present in the +S treatment than in the +A treatment, these vials had lower $^{14}CO_2$ production rates than the +A treatment vials throughout the experiment (*see Fig. 6*). Third, the presence of a growing bacterial inoculum in the +A vials was inconsistent with decreasing $^{14}CO_2$ production rates over the time-course (Fig. 7). Finally, bacterial metabolism would likely be depressed at the experimental temperature of 4°C.

Based on the above arguments, we assumed that bottle effects compromised rate measurements only after the first week when oxygen became significantly depleted. Hence, *Diporeia* incorporation, respiration, and excretion rates were calculated from points obtained during the first week. Also, use of only the initial time points for physiological rate estimations in the microcosm study is reasonable because *Diporeia* ingested mainly labeled algae of known specific activity at this time; incorporation, respiration, and excretion rates measured later in the time-course would be underestimated because the animals may have reingested fecal pellets with a lower specific activity.

The third assumption of comparable *Diporeia* feeding rates in the microcosm study and in the field is important in interpreting our results. Previous work (Gardner et al. 1989) indicates that *Diporeia* actively ingests carbon from the spring diatom bloom. Biogenic silica and the C-17 : C-29 *n*-alkane ratios, both indicators of the presence of algae, peaked in trap material collected during spring at this same study location. Importantly, the lipid content of *Diporeia* peaked shortly thereafter, implying relatively rapid and efficient incorporation of sedimenting algae by *Diporeia* during this period. Because the ratio of added algae to the animal density in the microcosm study approached that in the field, and because the animals rapidly assimilated and respired labeled C from the algae, we think that the feeding rates in these two environments were comparable. Further, the absence of substrate for burrowing in the +A treatment does not negate the comparability of rates measured in the +A microcosm with those in the field, as another study (Quigley et al. in prep.) indicated that average oxygen consumption rates were not significantly different for animals in test vials with and without a sand substrate.

Although reduced oxygen concentrations in the +S treatment vials had some effect on the observed [^{14}C]POC decomposition and $^{14}CO_2$ production rates, it was not likely large because microbially mediated anaerobic decomposition rates are not intrinsically lower than aerobic rates for most carbon sources (Foree and McCarty 1970; Henricks and Reeburgh 1987; Hansen and Blackburn 1991). However, sediment bacteria relying on externally supplied electron acceptors (i.e. nitrate and sulfate from the overlying water) may have been limited when these compounds were exhausted in the microcosms. Although bacterial metabolism may have been relatively slow at our experimental temperature (Pomeroy and Deibel 1986), the $^{14}CO_2$ production rate measured in the +S treatment could possibly have underestimated the true rate due to exhaustion of electron acceptors.

Decomposition, incorporation, respiration, and excretion rates—A simple linear model was fit to the initial time points ($t \leq 8$ d) to calculate rates (in nmol C cm^{-2} d^{-1}) of algal decomposition as well as rates for incorporation, respiration, and excretion by *Diporeia* and sediment bacteria (Table 3). Ingestion of the labeled algae by *Diporeia* was >27 times faster than algal decomposition mediated by the sediment microheterotrophs. In addition, the animals had a 23-fold higher respiration rate as compared to the bacteria without animals. The calculated release rate of [^{14}C]DOC by *Diporeia* and the net rate of [^{14}C]DOC release by sediment-associated bacteria were both small in comparison to the incorporation and respiration rates. The net release of labeled DOC by the bacteria was arbitrarily estimated as the [^{14}C]DOC remaining after the first 2 weeks in the +S treatment. Based on these rates, we conclude that the bulk of algal C reaching the sediment surface is likely ingested by *Diporeia* and subsequently incorporated into biomass

Table 3. Areal rates (in nmol C cm^{-2} d^{-1}) of algal ([^{14}C]POC) decomposition, ^{14}C incorporation, respiration of $^{14}CO_2$, and [^{14}C]DOC excretion-net release. The numbers in parentheses for *Diporeia* indicate the percentage of assimilation accounted for by incorporation, respiration, and excretion.

Rate	*Diporeia*	Bacteria
Algal ([^{14}C]POC) decomposition	50	1.8
Incorporation	17	—
(^{14}C *Diporeia*)	(35%)	
Respiration	29	1.3
($^{14}CO_2$ production)	(60%)	
Excretion-net release	2.7	0.5*
([^{14}C]DOC production-residual)	(5%)	

* Net [^{14}C]DOC remaining after first 2 weeks.

or respired and that only a small portion was remineralized by bacteria in these surficial sediments. Although not measured here, significant incoming organic C would also be directly or indirectly incorporated into other benthic animals, such as oligochaetes (Robbins et al. 1989).

The "assimilation" rate of algal C by *Diporeia,* calculated as the sum of observed incorporation, respiration, and excretion rates, was ~49 nmol C cm^{-2} d^{-1}. This approach was taken because ingestion rates, needed for more conventional estimates of assimilation, were not measured in the microcosm study. Of the total algal C assimilated, 60% was respired, 35% was incorporated into biomass, and 5% was accounted for as DOC (Table 3). The incorporation efficiency of 35% is near the low end of the range of growth efficiency (roughly equivalent to incorporation efficiency) of 30–60% reported for the *Diporeia* population in other locations in the Great Lakes (Johnson and Brinkhurst 1971). Our results differ somewhat from those previously calculated for *Hyalella azteca,* another freshwater amphipod, feeding on surficial sediments (Hargrave 1971); of the organic C assimilated, *Hyalella* respired 48%, incorporated 15%, and excreted 36%. These differences could be related to such factors as the quality of available food (fresh algae vs. sediments), different metabolic strategies of the two species, or may also be a consequence of different experimental methods.

Although published assimilation efficiencies are not available for *Diporeia,* the amphipods *Pontoporeia affinis* and *Pontoporeia femorata* assimilated roughly 40% of organic C in surficial sediments collected during the spring in the Baltic Sea (Lopez and Elmgren 1989). The few values available for other amphipods range between 5 and 92% for a suite of carbon sources including algae and surficial sediments (Hargrave 1970*a,* 1971; Lopez and Levinton 1987; Dermott and Corning 1988). This large range highlights the importance of food quality in controlling the assimilation efficiency of benthic macrofauna, in addition to probably reflecting widely different experimental approaches. If we assume an assimilation efficiency of 30% (Quigley unpubl. data), the three *Diporeia* in each microcosm vial ingested ~500 nmol C d^{-1}. This amount of algal C was sufficient to support almost 3 d of ingestion—the time period used in the rate and budget calculations. After this time, the animals were presumably recycling fecal pellets.

Algal carbon budget—The balance between calculated algal C input and losses integrated over the spring bloom period (78 d) is shown in Fig. 9. *Diporeia* assimilation (corrected for densities in the field) and microbially mediated algal decomposition accounted for ~61% (38 mmol C m^{-2}) and ~2% (1.4 mmol C m^{-2}) respectively, of spring algal C. The estimated *Diporeia* assimilation is expected to be among the highest in Lake Michigan owing to near maximal numbers of these animals at this site. This value for *Diporeia* may overestimate the true value because of the relatively small areal density of animals in the microcosms relative to that for the field. The availability of algal C per animal may decrease with increasing densities of animals. However, this result may not be an important consideration because the ratio of algae to animals in the microcosm study approached that in the field. Of the total C assimilated by *Diporeia,* somewhat more than half (60%) was respired, whereas most of the remaining C (35%) was incorporated into biomass. Apparent "excretion," as measured in the microcosm study, accounted for a very small fraction (~5%) of the assimilated C. Sediment microheterotrophs decomposed considerably less of the added algal C than did *Diporeia* in the microcosm study. The burial rate of organic C is essentially zero despite measurable organic C due to the lack of recent net sediment accumulation at this site.

On the basis of these estimates, *Diporeia* could be responsible for a large fraction of benthic respiration at this site (up to 96% of our measured CO_2 production). Although the accuracy of our estimate may be affected by a

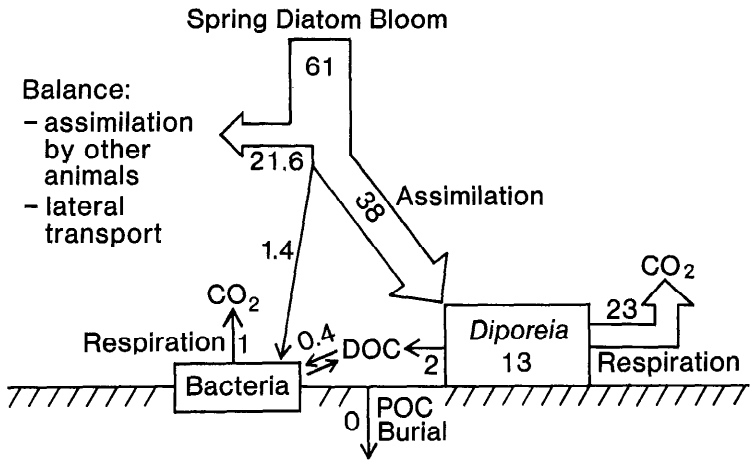

Fig. 9. Budget for spring algal C for nearshore Lake Michigan. Numbers associated with arrows or in boxes are fluxes for the spring bloom period of 78 d and have units of mmol m^{-2} (i.e. mmol m^{-2} d^{-1} × 78 d). The balance of algal C that is not accounted for by *Diporeia* assimilation or bacterial uptake is likely either taken up by other benthic animals or transported laterally to deeper portions of the lake (*see text*).

number of assumptions (*see above*), it is consistent with the conclusion of Gardner et al. (1985) that *Diporeia* is likely responsible for a large fraction of the mineralization of "fresh" detritus in the hypolimnion and surficial sediments of Lake Michigan. This conclusion was based on a comparison of estimated food requirements of the *Diporeia* population with calculated inputs of C measured with summer sediment traps. Also, the high percentage of the total benthic respiration associated with macrofauna found in the present study is near the high end of the reported range for boreal marine locations where macrofaunal respiration accounts for ~20–95% of the total (summarized by Grebmeier and McRoy 1989). In contrast, benthic invertebrate respiration was ~16% as large as that for sediment bacteria in Mirror Lake, New Hampshire (Wetzel 1983). Importantly, a boreal system such as Lake Michigan appears to be more comparable to tropical rather than temperate systems; benthic macrofauna in boreal and tropical systems can immediately utilize spring algal C because they are acclimated to the ambient temperature. In contrast, macrofauna in temperate systems often show a lag between the spring bloom and ingestion by benthic macrofauna because the animals are not yet active (G. Lopez pers. comm.). These results suggest that benthic energy transformations in the Lake Michigan ecosystem may resemble those of boreal (and even tropical) marine systems more than those of small lakes. These data support the conclusion that communities of benthic animals adapted to deep, oxygenated, cold environments not only thrive, but can play a major role in total benthic metabolism (Gardner et al. 1990).

A third (21.6 mmol C cm^{-2}) of the spring algal C was apparently not assimilated by *Diporeia* or remineralized by sediment microheterotrophs. This positive balance in the budget is reasonable because the sediment traps may have overestimated the algal C flux, *Diporeia* assimilation or microbially mediated algal decomposition estimates may have been biased, and other unquantified terms, including uptake by other organisms or lateral transport, were not included.

Algal inputs calculated from trap fluxes could have been overestimated due to resuspension. Resuspension of sediments is a ubiquitous phenomenon in Lake Michigan which confounds estimates of fresh C inputs to benthic environments using near-bottom traps. Resuspended material could account for ~100% of the trap material based on the ratio of ^{137}Cs in trap material and surficial (0–1 cm) sediments (unpubl. data). Algae-specific C fluxes were used in our budget to estimate inputs of fresh, readily metabolized C that is driving benthic metabolism. Although large diatoms are heavy, it is possible that some portion of these cells may have been resuspended, resulting in an overestimate of the algal C flux.

Algal C fluxes were larger in traps deployed 5 m off the bottom in comparison to those at 15 m off the bottom (unpubl. data), indicating that resuspension of algal cells increases with proxmity to the sediment surface.

Diporeia assimilation rates could have been under- or overestimated due to errors in our estimates of the *Diporeia* population or potential bottle effects on observed *Diporeia* incorporation, respiration, and excretion rates. Because the rates measured in the microcosm study are multiplied by the areal density of *Diporeia,* uncertainty in this value could significantly affect the balance. *Diporeia* areal density at this station is the only value in the budget that was not measured in 1990. The reported number (11,384 m^{-2}) is for 1988, the most recent year for which data are available. The density of *Diporeia* at this location, as well as that at other sites in Lake Michigan, varies on short-term (seasonal), medium-term (yearly), and long-term (decade) scales (Nalepa 1987; Quigley and Lang unpubl. data). The differences of ~30% that exist between estimates made in the early 1960s and those made in the early 1980s are nearly matched by interannual variations in *Diporeia* density of ~27% in the last half of the 1980s (Nalepa 1987; Quigley and Lang unpubl. data). Increasing the population size by 30% results in an estimated areal carbon assimilation of ~50 mmol cm^{-2} for the spring bloom period.

Potentially important bottle effects on observed *Diporeia* assimilation rates include lack of axenic conditions and a decrease in oxygen concentration as already discussed, in addition to possible buildup of toxic metabolites. If important, these conditions would result in underestimated assimilation rates for *Diporeia. Diporeia* incorporation and respiration rates were calculated using only the initial few time points before appreciable changes would have occurred to prevent bias due to the potential oxygen stress or the buildup of toxic metabolites. Thus it seems likely that *Diporeia* assimilation rates measured in the first 2 weeks of the microcosm study may have reasonably reflected field conditions.

Microbially mediated decomposition may have been underestimated in our study because it was measured in the absence of *Diporeia* and other macrobenthos. Hargrave (1970*b*) noted that bacterial metabolism was significantly stimulated at high amphipod (*H. azteca*) population densities. Microbial turnover rates and biomass were both enhanced on particles egested by *Orchestia grillus,* an amphipod (Lopez et al. 1977). In their review, Tenore et al. (1982) identified possible mechanisms whereby microbial metabolism is stimulated in the presence of benthic macrofauna. Shredding of large food particles by benthic macrofauna increases the surface area available for microbial exoenzymatic attack. Fecal pellets serve as colonization sites for bacteria and often are sites of stimulated bacterial metabolism compared to that in bulk sediment. Finally, bioturbation stimulates bacterial metabolism by mixing both fresh, high quality C sources and electron acceptors (oxygen, nitrate, sulfate, etc.) into the sediment.

Quantitatively significant unidentified loss terms include C uptake by other macrofaunal species, including oligochaetes, sphaeriid bivalves, and chironomids, that may compete or otherwise interact with *Diporeia. Stylodrilus heringianus,* an oligochaete, and tubificids (likely *Limnodrilus* spp.) are abundant (2,400 and 2,200 ind. m^{-2}, respectively, at the study site; Nalepa et al. 1985). Abundances of tubificids in Lake Erie were directly proportional to annual inputs of organic C to the sediments (Robbins et al. 1989). In addition, meiofaunal species including nematodes, harpacticoids, tartigrades, and ostracods occur in surficial sediments from nearshore Lake Michigan (Nalepa and Quigley 1983). Most of these species would have been retained on the 63-μm sieve and therefore removed from the sediments, while the smaller, more delicate species that were not retained may have been damaged during the sieving procedure. Both possibilities would result in an underestimation of C metabolism in the +S treatment and therefore a positive balance in the budget. Aggregate metabolism of meiobenthos can be up to five times greater than that for macrobenthos relative to dry weight (Gerlach 1971). Based on the observed abundance of meiofauna in Lake Michigan and published metabolic rates, Nalepa and Quigley (1983) estimated that meiofaunal metabolism could amount to between 33 and 80% of macrofaunal metabolism. If meiofaunal metabolism is 57% of that for macrofauna, then all of the "extra" ~21% of the deposited algal C would be accounted for.

Physical processes may also remove or bring metabolizable C into the sample region. The

study site is located in the slope region of eastern Lake Michigan, an area characterized by upwelling events occurring at a frequency of ~4–5 d in spring and by maximal fluxes of resuspended sediments and significant downslope transport (Eadie et al. 1984). It is likely that some of the algal C deposited during the spring bloom is resuspended and eventually redeposited in deeper locations in the lake. Given that no measurable net sediment accumulation occurs at the study site despite the large C (both algal and total) influx, resuspension and lateral transport are plausible processes that could help explain our observations. Despite these uncertainties in our estimates, it is reasonable to conclude that direct uptake and incorporation of phytoplankton C by *Diporeia* is an important coupling mechanism between pelagic and benthic regimes that will minimize energy losses through trophic transfer in the system. Because *Diporeia* is a favored prey item among several Great Lakes forage fish (Wells 1980), algal C is transferred to fish with only one intervening trophic step. Thus ~21% of the algal C reaching the benthos is incorporated into *Diporeia* biomass and is available for fish. This incorporated fraction represents an ecological efficiency (percentage of transfer of energy from one trophic level to the next) of 21%, somewhat higher than the reported range of 5–15% (Wetzel 1983). This result is reasonable because metabolic losses would be minimized at the relatively low temperature of the *Diporeia* habitat. Thus the link between spring phytoplankton and *Diporeia* appears to be efficient, with relatively low loss of energy to physiological maintenance and to detrital carbon pools.

The above results indicate that the magnitude of the rates measured in the field and in the microcosm study are similar. They suggest that *Diporeia* assimilation is likely a quantitatively more important pathway for algal carbon from the spring diatom bloom than is bacterial metabolism in surficial sediments at this site.

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Submitted: 10 February 1992
Accepted: 10 September 1992
Revised: 18 November 1992